Asking the auditory cortex the right question

Recordings in different parts of the cortex are beginning to reveal how animal communication calls are analyzed by the brain.

Despite the importance of auditory regions of the cortex in the perception of communication sounds — including human speech — we still have a very incomplete understanding of how biologically relevant features of complex sounds are processed at this level of the brain. The auditory cortex is found in the temporal lobe and consists of a primary field, AI, together with several surrounding areas which can be distinguished on the basis of their cytoarchitecture, connections and physiological response properties [1,2]. Area AI receives the largest thalamocortical projection and is characterized by a systematic mapping of sound frequency across one of its dimensions. This tonotopic organization mirrors the variation in frequency tuning found among hair cells located at different points along the length of the cochlea, and is also seen in some of the other cortical areas.

It was recognized thirty years ago that although cortical neurons respond to a large variety of stimuli, they often prefer more complex sounds to pure tones [3]. It therefore seems likely that a successful approach to understanding the functions of the cortex will be to probe the responses of its neurons with natural sound sources, rather than providing a description of how neurons encode the physical dimensions of simple sounds such as the frequency and amplitude of pure tones [4]. Indeed, the most complete descriptions of the functional organization of the auditory cortex or its non-mammalian equivalent have come from neuroethological studies, which have revealed the existence of neurons that are tuned to behaviourally important acoustical signals in song birds [5] and echolocating bats [6]. But in mammals with less stereotyped auditory behaviour, it is more difficult to identify the most appropriate stimulus for auditory cortical neurons from the huge range of potentially interesting sounds.

Complex sound analysis in the mammalian auditory cortex

Most biological communication signals, including human speech and other complex sounds, such as music, are characterized by complex spectra — the distribution of energy as a function of frequency — and by variations in amplitude and frequency composition over time (Fig. 1). Because of the large number of parameters involved, an intermediate approach to the study of auditory responses to natural vocalizations is to examine whether cortical neurons respond selectively to particular aspects of these signals, such as spectral content or temporal modulation. In the cochlea, each audible frequency is represented at a different point along the one-dimensional receptor surface. But in area AI, neurons that are tuned to the same sound frequency form slabs that extend into the depth of the cortex and tangentially across its surface in a direction approximately orthogonal to the tonotopic axis. In cats, several response properties, including the bandwidth and shape of the frequency response profiles [7–10] and the sensitivity to frequency-modulated sounds [9–11] vary systematically across the isofrequency regions. The idea that information is processed in AI within frequency-specific channels must be treated with caution following the demonstration that the spatial distribution of neurons activated by a given stimulus changes markedly with sound level, and may extend well beyond a single isofrequency channel [12]. Nevertheless, these response properties and the recently described sensitivity of cat AI neurons to the spectral profile of broadband sounds [13] appear to be suited to extracting the spectral peaks and gradients that are features of a number of natural communication sounds, including the harmonic structure of human vowels.

Functional specialization beyond the primary cortex

In addition to this role in the preprocessing of vocalization sounds, AI is also involved in the analysis of other attributes of sound sources, including their amplitude and location. Following the principles that operate in the visual system, we might expect other cortical fields that, on the basis of their connectivity patterns, occupy a higher level than AI to contain neurons with more specific stimulus requirements, and that there may be one or more areas that are particularly concerned with the processing of communication signals. Although there are

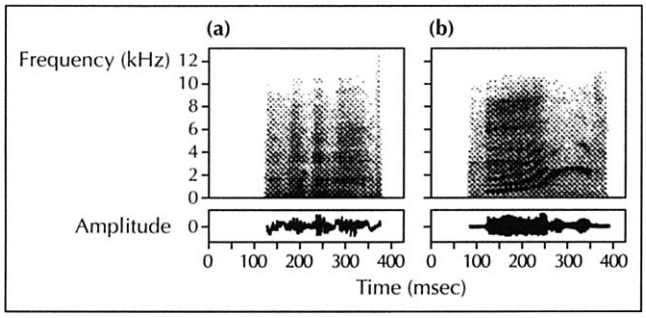

Fig. 1. Examples of rhesus monkey vocalizations. The upper traces are spectrograms showing the variation in amplitude (represented by the darkness of the trace) across frequency and over time. The lower traces represent the waveforms of these vocalizations, showing how the amplitude (summed across all frequencies) changes as a function of time. **(a)** Call dominated by noisy components. **(b)** Call containing several harmonic components. These calls have a similar duration and overall bandwidth, but vary in their acoustic structure. Modified from [20].

some indications that temporal response properties vary among different auditory fields in the cat cortex [14,15], the best evidence that separate auditory areas have distinct roles in processing biologically important acoustic signals has come from studies of the echolocating mustached bat. Suga and colleagues [6] have shown that cortical neurons in fields outside AI are tuned to particular combinations of different harmonic components of the bat's orientation sonar pulse and its Doppler-shifted echo. The pairs of sounds to which the neurons are tuned vary systematically across the cortical surface to form neural maps of biosonar information, including the range and relative velocity of objects in the bat's flight path.

Functional imaging studies in human subjects have provided evidence that certain cognitive tasks related to the perception of language and music are lateralized to different regions of the cortex [16–19]. For example, although speech sounds activate the temporal lobes bilaterally, word comprehension and analysis of phonetic structure may particularly involve Wernicke's area and Broca's area, respectively, in only the left hemisphere [16,18]. Evidence for equivalent areas associated with the processing of communication calls in other primates is missing and, at present, we know very little about the functional organization of neurons in non-primary areas of the cortex.

In a recent study, Rauschecker *et al.* [20] examined the response properties of neurons in the non-primary lateral belt region of the auditory cortex of the rhesus monkey (Fig. 2). Working with an analogy to the situation in the visual system, where neurons in extrastriate visual cortex have larger receptive fields and more specific stimulus requirements than those in the primary visual area, they used a combination of band-passed noise and digitized monkey calls as their stimuli. The majority of neurons they recorded from responded better to band-passed noise than to pure tones, suggesting that their inputs had been integrated over a range of frequencies. This observation has also been made for other levels of the auditory system outside the primary ascending pathway.

Rauschecker and colleagues went on to examine the selectivity of lateral belt neurons to noise bursts by varying the bandwidth and the centre frequencies of the stimuli. They found that a 'best' centre frequency could be ascribed to each neuron. This remained largely unchanged for electrode penetrations that extended radially into the depth of the cortex, but varied across its surface. Although their data set was fairly limited, they observed two reversals in the orderly progression of best centre frequencies: the values decrease, then increase, and finally decrease again in a rostro-caudal direction. The functional borders of auditory cortical fields are often difficult to determine electrophysiologically, and a reversal in frequency gradient is regarded as an important criterion for identifying the boundary between different areas. These results therefore suggest that three tonotopic areas exist within the lateral belt region of the macaque superior temporal gyrus, although verification of this, and equivalence between tonotopically distinct regions and anatomical subdivisions of this region that have been reported previously [2], will require an examination of their connections and cytoarchitecture.

Rauschecker and colleagues also found that the preferred bandwidths of the noise stimulus varied topographically in a medio-lateral direction — that is, orthogonal to the axis of best centre frequencies. This two-dimensional arrangement of response preferences resembles that described for AI, with the important exception that the organization of the lateral belt areas only became

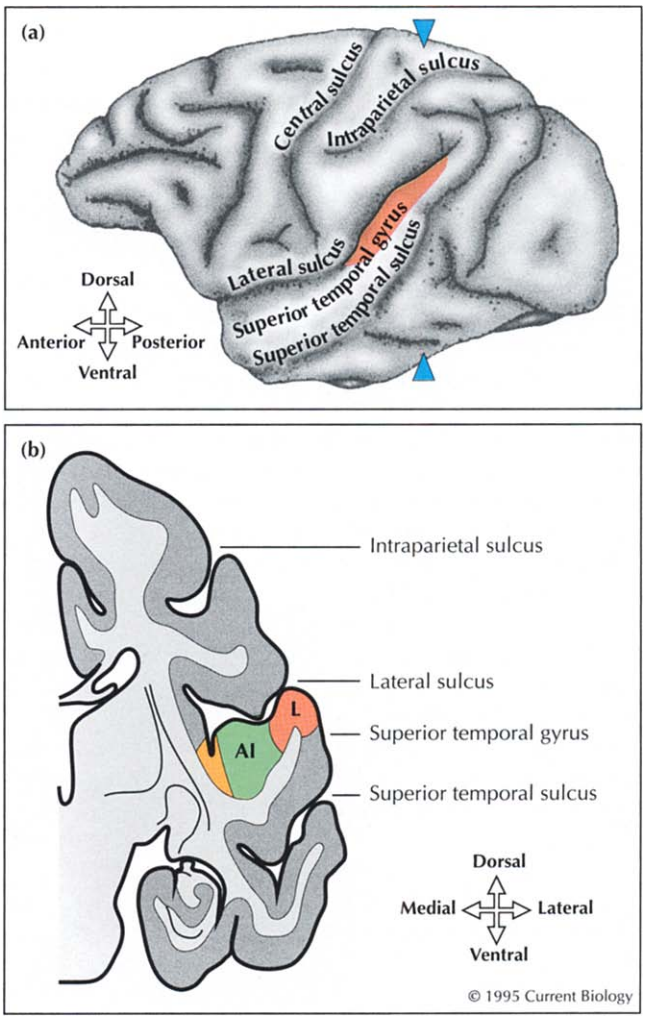

Fig. 2. **(a)** Lateral view of the left cerebral hemisphere of the rhesus monkey. The area shown in dark pink indicates the location of the lateral belt region on the exposed surface of the superior temporal gyrus. **(b)** Coronal section through the hemisphere at the level indicated by the blue arrowheads in (a). The primary auditory cortex, AI (green), lies on the caudal superior temporal plane, deep within the lateral sulcus. It is therefore hidden from view by the overlying parietal cortex. A belt of cortex comprising several cortical fields lies adjacent to AI (orange and dark pink). The detailed parcellation of these non-primary fields is currently uncertain [2]. The lateral belt region, L (dark pink), which probably consists of several different areas, extends laterally alongside AI on the superior temporal plane and round onto the exposed lateral bank of the superior temporal gyrus.

apparent when band-passed noise stimuli, rather than pure tones, were used.

Several studies have examined the responses of primate auditory cortical neurons to species-specific vocalizations, in which the signal amplitude can vary both across frequency and over time (Fig. 1; see [1] for review). Recordings were made from AI in most of these studies, and these revealed that the majority of neurons respond to such sounds, although few are tuned to particular calls. It therefore seems likely, as concluded by Steinschneider *et al.* [21] from their analysis of responses in monkey AI to speech sounds, that the complex acoustic signals that characterize communication calls are encoded at this level of the cortex by the overall spatio-temporal pattern of activity across many neurons.

Because of the possible homology between the lateral belt region of the rhesus monkey cortex and the comparable part of the human superior temporal gyrus — an area that may be particularly involved in speech perception — Rauschecker and colleagues [20] also examined the responses of these neurons to a series of energy-matched vocalizations. They reported that nearly 90 % of the neurons tested within the three tonotopic regions of the lateral belt exhibited a level-independent preference for certain types of call. In most cases, however, this selectivity of response was rather weak and, according to their criteria, only 7 % of these units strongly preferred one particular call. Nevertheless, the neurons did respond better to most types of vocalization than to energy-matched tonal or band-passed noise stimuli, indicating the importance of the spectral and/or temporal structure of the call in eliciting a response.

It is important to determine whether tuning to conspecific vocalizations can be explained in terms of the sensitivity of the lateral belt neurons to simpler, artificial stimuli. In some neurons, responses to different frequency components of the calls matched the frequency-selectivity revealed with band-passed noise. More interestingly, other neurons gave much greater responses to complete calls than to the filtered components, suggesting that the preference for these stimuli may derive from non-linear facilitatory mechanisms, arising either within the lateral auditory fields or at an earlier stage of processing. Similar findings have also been reported for neurons that encode biosonar information in the cortex of the echolocating bat [6] and for song-selective neurons in the avian forebrain [5].

Demonstrating selectivity to complex acoustic stimuli is problematic because of the large number of signals to which a cortical neuron may potentially respond. A neuron may appear to favour one particular stimulus only because other sounds that may be equally effective have not been tested. Conversely, a lack of specificity may reflect the absence of the one really effective cue from the stimulus set. It also seems likely that responses to communication calls will depend on their behavioural relevance and the context in which they are presented. Employing an optimization search procedure [22] may help in determining stimulus preferences by identifying the combination of parameters that evoke the best response, although the usefulness of this approach may be limited by the nonlinear summation exhibited in both the frequency and time domains by auditory neurons in the lateral belt region of the superior temporal gyrus.

Notwithstanding these considerations, the data presented by Rauschecker *et al.* [20] suggest that the lateral belt neurons are not highly specialized feature detectors, each responding exclusively to a particular communication call. Their response properties suggest that it is more appropriate to regard them as filters that are tuned to elements of these biologically important signals — but what these elements are remains to be determined. This type of neural code, in which the calls are presumably represented by different patterns of activity across an ensemble of neurons, would seem to be more consistent with the large repertoire of rhesus monkey vocalizations, and particularly of human speech sounds. It would clearly be of interest to know whether the preference of neurons for particular types of macaque call varies within or between the three tonotopic areas identified by Rauschecker *et al.* [20] with band-passed noise, and whether there are any differences between the two hemispheres. Moreover, confirmation that communication sounds are processed in a hierarchical sequence will require a careful comparison of the response properties of neurons in different cortical areas.

Plasticity in the neural representation of complex sounds

Although counting action potentials is the usual index used by neurophysiologists to measure the responsiveness of sensory neurons, there is increasing evidence that synchronized discharges between different neurons may allow more precise coding of information and a means of linking activity in different parts of the brain. Moreover, changes in the strength of coupling appear to be associated with the reorganization of cortical representations that accompany improvements in perceptual performance [23]. Given the lack of evidence for individual vocalization detectors, it is possible that communication calls are represented by synchronized responses in distributed networks of cortical neurons. Learning to discriminate and categorize new complex sound patterns, produced by members of the same or different species, may then be accompanied by remodelling of these functional connections.

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Andrew J. King, University Laboratory of Physiology, Parks Road, Oxford OX1 3PT, UK.